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Focus paper

There is no such thing as the ‘Ediacara Biota’



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ABSTRACT

The term ‘Ediacara Biota’ (or many variants thereof) is commonly used to refer to certain megascopic fossils of Precambrian and early Palaeozoic age – but what does the term actually mean? What differentiates a non-Ediacaran ‘Ediacaran’ and an Ediacaran ‘Ediacaran’ from an Ediacaran non-‘Ediacaran’? Historically, the term has been used in either a geographic, stratigraphic, taphonomic, or biologic sense. More recent research and new discoveries, however, mean that the term cannot actually be defined on any of these bases, or any combination thereof. Indeed, the term is now used and understood in a manner which is internally inconsistent, and unintentionally implies that these fossils are somehow distinct from other fossil assemblages, which is simply not the case. Continued use of the term is a historical relic, which has led in part to incorrect assumptions that the ‘Ediacara Biota’ can be treated as a single coherent group, has obscured our understanding of the biological change over the Precambrian–Cambrian boundary, and has confused research on the early evolution of the Metazoa. In the future, the term ‘Ediacaran’ should be restricted to purely stratigraphic usage, regardless of affinity, geography, or taphonomy; sufficient terminology also exists where reference to specimens on a geographic, taphonomic, or biologic basis is required. It is therefore time to abandon the term ‘Ediacara Biota’ and to instead treat equally all of the fossils of the Ediacaran System.

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1. Introduction

Despite the discovery of Precambrian fossils in England in 1848 (Eskridge, 1868; Ford, 2008), in Newfoundland in 1868 (Billings, 1872; Gehling et al., 2000), and in Namibia in 1908 (Gürich, 1929; Grazhdankin and Seilacher, 2005; Vickers-Rich et al., 2013), the prevailing orthodoxy in the first half of the 20th century held that strata older than Cambrian in age were uniformly devoid of evidence of life. It was thus the case that upon the discovery of fossils in the Ediacara Hills, Flinders Ranges, South Australia, by Reg Sprigg in 1946 (Sprigg, 1947, 1948, 1949; see also Turner and Oldroyd, 2009), the host strata were automatically presumed to be early Cambrian in age. It was only with the rediscovery of fossils in undoubtedly Precambrian strata in England in 1957 (Ford, 1958, 2008)

that it was realised that these Australian fossils were older than had initially been presumed.

Principally through the efforts of Prof. Martin Glaessner (Glaessner, 1958, 1959; Glaessner and Dailly, 1959), the Australian fossils rapidly became internationally famous, with descriptions extending beyond academic journals into the pages of popular-science publications such as *Scientific American* (Glaessner, 1961). Since then, purportedly similar fossil assemblages have been found in numerous localities worldwide, including Russia, Canada, and the United States (reviewed by Waggoner, 1999; see also Narbonne, 2005; Xiao and Laflamme, 2009). It is testament to the work of Glaessner and his colleagues that, despite both this worldwide distribution and the prior discovery of Precambrian fossils elsewhere, such fossils are now generally referred to as the ‘Ediacara Biota’.

But what does this phrase actually mean?

2. The rise of the ‘Ediacara Biota’ term

Several different variants of the term ‘Ediacara Biota’ have been used over the past several decades – including ‘Ediacara Fauna’, ‘Ediacaran Fauna’, ‘Ediacarian Fauna’, ‘Ediacara Biota’, ‘Ediacaran Biota’, ‘Vendian Fauna’, ‘Vendian Biota’, ‘Ediacara(n) fossils’,

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'Ediacara(n)-type fossils', and referring to the fossils as 'Ediacaran' – often with quite different meanings.

The first usage of such nomenclature appears to have been by [Glaessner \(1958\)](#), who referred to the Flinders Ranges fossils – then still thought to be lower Cambrian in age – as the 'Ediacara Fauna'. However, the phrase rapidly became the preferred term to refer more broadly to the purportedly similar fossil assemblages worldwide, in addition to the Australian fossils. For example, [Fischer \(1965, p. 1206\)](#), in discussing whether any known fossils were Precambrian in age stated: "*The Ediacara fauna deserves special consideration... Elements of this fauna occur in Africa, Europe, and North America*", and [Zaika-Novatskiy et al. \(1968\)](#) described the "*First member of the Ediacara Fauna in the Vendian of the Russian Platform*". [Glaessner \(1971\)](#) himself soon adopted this expanded meaning, noting, for example, that "*the most numerous finds of fossils belonging to the Ediacara fauna have been made in South-West Africa in the Kuibis Quartzite of the Nama Series*" (p. 509). Such usage still persists today; e.g. "*Some representatives of the Ediacara fauna have been later re-interpreted as pseudofossils*" ([van Loon, 2008, p. 175](#)); "*The first appearance of Ediacara fauna is thought to have followed the last of the ~750–635 Ma Neoproterozoic glacial episodes by 20–30 million years*" ([Meert et al., 2011, p. 867](#)).

The 'Ediacaran Fauna' spelling variation was introduced by [Cloud and Abelson \(1961\)](#) ("*the diversified Ediacaran fauna of South Australia is at its oldest very late Precambrian and may well be early Cambrian*"; p. 1706), and also continues to be used today – e.g. "*It is uncertain whether the Ediacaran fauna was the spark of biological diversity that ignited the following Cambrian explosion or was an evolutionary experiment that ended in extinction*" ([Li et al., 1998, p. 879](#)); "*Increasing oxygenation of the upper ocean and atmosphere following the Marinoan glaciation is thought to have triggered the development of the Ediacaran fauna*" ([Wille et al., 2008, p. 769](#)); "*Within the Ediacaran fauna, several different morphological and constructional clusters can be distinguished, although the extent to which they represent monophyletic clades is unclear*" ([Erwin, 2009, p. 2257](#)).

More recently, the term(s) 'Ediacar(i)a(n) Biota' have gained preference, over 'Ediacar(i)a(n) Fauna' – e.g. "*Fossils of the terminal Proterozoic Ediacara biota are found on most continents*" ([Gehling, 1999, p. 40](#)); "*The Ediacara Biota: Neoproterozoic Origin of Animals and Their Ecosystems*" ([Narbonne, 2005, p. 421](#)); "*these traces are directly associated with an Ediacara biota*" ([Liu et al., 2010, p. 125](#)).

The terms 'Vendian Fauna' and 'Vendian Biota' have also been used, principally by Russian geologists and palaeontologists, but also by others – e.g. "*the comparison of patterns of change in the Vendian biota relating to the Varangerian glacial event is severely hampered by the difficulty of detailed correlation of packages of late Neoproterozoic strata*" ([Vidal and Moczyłowska, 1995, p. 208](#)); "*Obstacles to considering the "Vendobionta" as early metazoans include the time gap between the disappearance of Vendian biotas and the appearances of Cambrian faunas, the lack of Vendian-type organisms in the Cambrian and later Lagerstätten, and supposed morphological disparity between most Vendian organisms and their Phanerozoic successors*" ([Waggoner, 1996, p. 190](#)); "*the circumstantial evidence of an early history of phylogenesis seems persuasive, in spite of an absence of obvious 'ancestors' among the soft bodied fossils of the late Precambrian Vendian fauna*" ([Cooper and Fortey, 1998, p. 152](#)); "*The Vendian biota of Namibia comprises an assemblage of forms, exotic to mainstream biology, dominated by serially quilted body plans*" ([Grazhdankin and Seilacher, 2005, p. 571](#)); and the title of ICGP Project 493 – "*The Rise and Fall of the Vendian Biota*".

It is safe to assume that [Glaessner \(1958\)](#) initially used the term 'Ediacara Fauna' to refer solely to the fossil assemblages of the Ediacara Hills localities (the *geography-based* definition). Why this term (and similar terms) became used to refer to other fossils

worldwide is less clear, but it is likely due to a combination of the age of the fossils (the only Precambrian megascopic remains known at that time), the broad faunal similarity of the other assemblages to the South Australian fossils (as distinct from later fossil communities), and perhaps most importantly, their taphonomic style. Indeed, the preservation of the fossils as moulds and casts in sandstones, a taphonomic style then thought to be unique to the Precambrian, would originally have seemed a compelling reason for considering such fossil assemblages as a single group (the *preservation-based* definition).

Glaessner and colleagues (summarised in [Glaessner, 1984](#)) regarded these fossils as ancestral members of modern metazoan phyla, and so no significant biological distinction was intended by the use of the term 'Ediacara Fauna'. However, biology may have played a role in the terminological shift from 'fauna' to 'biota'. A controversy over the biological interpretation of the fossils was sparked initially by [Seilacher \(1984, 1989, 1992\)](#), who proposed that they were not metazoans, but were rather members of an extinct Kingdom, the Vendozoa (later renamed Vendobionta by [Buss and Seilacher, 1994](#)). Subsequently, alternative non-metazoan interpretations as protists ([Zhuravlev, 1993](#)), fungi ([Peterson et al., 2003](#)), and, bizarrely, even lichens ([Retallack, 1994](#)), were proposed. It is possible that increased use of 'biota' in place of 'fauna' reflected such non-metazoan palaeobiological interpretations of the fossils – although it should be noted that the phrase 'Ediacara Biota' precedes the Seilacherian controversy (e.g. "*Annulated worms, medusoids, and frondlike fossils constitute most of the Ediacaran biota*"; [McMenamin, 1982, p. 290](#)). It is also quite clear that such interpretations led many authors to use the term 'Ediacara Biota' (or other variants) to imply that these fossils were somehow biologically distinct from later Cambrian organisms (the *biology-based* definition). Indeed, the fossils were often discussed in terms such as "*Alien Beings Here on Earth*" ([Lewin, 1984](#)), or "*The Ediacara Biota: A Terminal Neoproterozoic Experiment in the Evolution of Life*" ([Narbonne, 1998](#)).

Use of the 'Vendian Fauna/Biota' variation was due to the prior definition of the Vendian as the terminal System of the Precambrian on the Russian Platform (e.g. [Sokolov and Fedonkin, 1984](#), and references therein), and thus refers to the fossils in a stratigraphic sense, i.e. as the fossil biota of the 'Vendian System' (the *stratigraphy-based* definition). The use of the term Vendian has, however, decreased markedly since the official establishment of the Ediacaran as the terminal System of the Precambrian ([Knoll et al., 2004, 2006](#)), with the GSSP in South Australia.

This highlights a major problem: that, subsequent to the establishment of the Ediacaran System, the variant term 'Ediacaran Biota' may be used either in the sense that 'Ediacara Fauna' was originally used, or in a stratigraphic sense, to indicate the fossils of the Ediacaran System. These are not the same thing.

3. The fall of the 'Ediacara Biota' term

As discussed in the preceding section, the term 'Ediacara Biota' (note that subsequent use of the term 'Ediacara Biota' herein should be understood to equally refer to any of the variants of this term mentioned above) has been used in four senses – geographic, stratigraphic, taphonomic, and biologic. However, none of these four definitions has any remaining basis.

3.1. The geography-based definition

This ceased to have any basis as soon as the term 'Ediacara Fauna' was used to refer to fossils from assemblages other than that from the Ediacara Hills in South Australia.

3.2. The stratigraphy-based definition

It is possible that certain authors have used the term 'Vendian Biota' or 'Ediacaran Biota' in a purely stratigraphic sense; to indicate the fossils of the Vendian System or (more recently) the Ediacaran System. However, it is clear that this is not what is usually meant or understood by the term 'Ediacara Biota'. Such usage would, of course, include all fossils of Ediacaran age preserved in any taphonomic mode, including skeletal, phosphatised, and carbonaceous compression specimens. However, these have not generally been considered part of the 'Ediacara Biota' (see also Section 3.3).

Discussions of 'Ediacaran survivors' in Cambrian sediments (e.g. Crimes et al., 1995; Jensen et al., 1998; Crimes and McIlroy, 1999; Hagadorn et al., 2000; MacGabhann, 2007; MacGabhann et al., 2007; Laflamme et al., 2013;), and of pre-Ediacaran 'Ediacara Biota' fossils (e.g. MacGabhann, 2007; Meert et al., 2011), also make clear that the term is not generally used or understood in a purely stratigraphic sense.

3.3. The preservation-based definition

The view that the fossils of the 'Ediacara Biota' share a common mode of preservation is commonly held. However, this is simply not the case.

In the shallow marine siliciclastic sediments at Ediacara, South Australia, two modes of fossil preservation are common. These are:

1. **'gravity cast'** (MacGabhann, 2007) preservation as negative epirelief moulds on the top surfaces of sandstone beds, and corresponding positive hyporelief casts on the sole surface of the overlying beds, and
2. **'death mask'** (Gehling, 1999) preservation as negative hyporelief moulds on the sole surface of sandstone beds, with corresponding positive epirelief casts on the top surfaces of underlying beds.

The distinction between these modes of preservation is subtle, but may be extremely important. Preservation of an organism as a gravity cast fossil merely requires the moulding of the lower surface of the organism by underlying sediment; upon burial and decay, sand from the overlying bed simply moves downwards, under the force of gravity, to fill the mould and cast the fossil. 'Death mask' preservation, however, requires the mould to be formed by the burying sediment, and that this burying sediment be lithified (by early diagenetic mineralisation) and capable of holding the shape of the mould while the underlying sediment remains mobile and unconsolidated, as it moves upwards against the force of gravity to fill the mould and cast the fossil. The difference between these modes of preservation may imply significant differences in the properties of the organisms preserved in each style (Wade, 1968; Gehling, 1999).

Moreover, the most common form of fossil preservation in the Ediacaran siliciclastic sediments of Namibia is neither of these, but a third mode:

3. **'endorelief'** preservation of fossil moulds and casts entirely within siliciclastic event beds (Grazhdankin and Seilacher, 2002, 2005; Dzik, 2003; Narbonne, 2005; Elliott et al., 2011; Vickers-Rich et al., 2013).

A fourth distinct mode of preservation is exemplified by the fossils of the Mistaken Point Lagerstätte in Newfoundland, Canada. Here, fossils are preserved in:

4. **'Conception'** preservation (Narbonne, 2005), as fossil moulds and casts on bedding plane surfaces underneath beds of

volcanic ash (e.g. Benus, 1988; Narbonne and Gehling, 2003; Flude and Narbonne, 2008), so-called for the stratigraphic position of the majority of these fossils in the Conception Group.

Conception preservation has not, as yet, been studied in detail, and it is unclear if the taphonomic processes involved are similar to those in either gravity cast, death mask, or endorelief preservation. As noted by Bamforth et al. (2008) and Liu et al. (2010), both negative hyporelief and negative epirelief fossil moulds (with corresponding casts) are known in such preservation, and it is thus likely that at least 'death mask' and 'gravity cast' variations of Conception preservation exist.

It may be argued that although there are fundamental differences between each of these four taphonomic modes, they share a common product in the preservation of fossils as moulds and/or casts in clastic sediments. However, a fifth mode of fossil preservation does not:

5. **'Khatyspyt'** preservation, as moulds and casts in carbonate sediments, best known from the Khatyspyt Formation of Siberia (e.g. Vodanjuk, 1989; Grazhdankin et al., 2008; Shen et al., 2009).

The mechanisms involved in this taphonomic mode are even more poorly understood than Conception preservation, and it is likewise not yet known how this mode relates to the other styles discussed above. Indeed, it is entirely possible that Khatyspyt preservation actually incorporates carbonate variants of the death mask, gravity cast, and endorelief styles discussed above; or that geochemical processes are involved which are completely different from those which facilitate such preservation in siliciclastic sediments.

Fossils preserved in each of the five taphonomic modes considered above have been considered part of the 'Ediacara Biota'. By contrast, fossils from a sixth mode of preservation significant in the Ediacaran have not:

6. **'Burgess Shale-style'** preservation, as carbonaceous compressions (Xiao et al., 1998, 2002; Yuan and Cao, 1999; Zhao et al., 2004; Tang et al., 2006; Grazhdankin et al., 2007; Tang et al., 2008a,b; Zhu et al., 2008; Yuan et al., 2011; Cai et al., 2012; Van Iten et al., 2013).

A seventh group of fossils of Ediacaran age have likewise never been considered part of the 'Ediacara Biota':

7. **Skeletal fossils**, such as *Cloudina*, *Namacalathus*, and *Sinotubulites* (e.g. Germs, 1972; Grotzinger et al., 2000; Amthor et al., 2003; Chen et al., 2008; Wood, 2011).

This list of seven Ediacaran taphonomic styles is, of course, an oversimplification, as taphonomic processes vary based on sedimentary provenance and geochemistry, environmental conditions (Eh, pH, temperature, salinity), microbiological populations, sedimentary depositional processes, and many other factors. Each of these listed taphonomic modes thus should essentially be considered as a suite of related taphonomic variants. It is also highly likely that sets of apparently similarly-preserved specimens may actually have been produced by differing taphonomic pathways which coincidentally produce similar results (e.g. the preservation of certain positive hyporelief fossils may have been aided by 'death mask' style processes, while others may have been produced without the aid of early diagenetic mineralisation). Nor have all taphonomic modes known from the Ediacaran been considered above: fossils preserved by processes such as phosphatisation (Xiao

and Knoll, 1999; Yin et al., 2007) may be rarer, but are also known, and provide significant palaeontological evidence.

Previous authors have included only specimens preserved as moulds and casts (in both siliciclastic and carbonate sediments) in the 'Ediacara Biota'. For example, Laflamme et al. (2013, p. 559) stated: "we restrict the term *Ediacara biota* to refer to lineages of large, soft-bodied organisms preserved as casts and molds in sediments of *Ediacaran* (and perhaps *Cambrian*) age". Such definitions consider the term 'Ediacara Biota' to comprise all fossils preserved in death mask, gravity cast, endorelief, Conception, and Khatyspyt styles: but only these styles, excluding Burgess Shale-style carbonaceous compressions, phosphatised or skeletal specimens, and remains preserved in other taphonomic modes.

However, such a distinction is simply not possible, for one simple reason: organisms can be preserved as fossils in more than one taphonomic mode.

For example, in the *Ediacaran* White Sea Lagerstätte in Russia, while most specimens are preserved in death mask, gravity cast, and endorelief styles, carbonaceous preservation of so-called 'Ediacara-type' fronds is also known (Steiner and Reitner, 2001). A second example is the eight-armed fossil *Eoandromeda*, which is known preserved as Burgess Shale-style carbonaceous compressions in the Doushantuo Formation of South China, and apparently in gravity cast-type preservation at *Ediacara* in South Australia (Tang et al., 2008a,b; Zhu et al., 2008).

By Laflamme et al. (2013)'s definition above, as well as common usage, the 'Ediacara Biota' includes neither the Chinese specimens of *Eoandromeda*, nor the White Sea carbonaceous fronds, despite the fact that specimens conspecific to both are included. Should we, then, extend this definition to include such specimens? If not, why not? Clearly, both *Eoandromeda* from *Ediacara* and fronds from the White Sea preserved purely as sandstone casts are included in the 'Ediacara Biota', so why exclude specimens of the same species which are preserved in a different way?

But if we do extend the definition to include Burgess Shale-style fronds and *Eoandromeda*, then what justification could be used to exclude other specimens preserved as Burgess Shale-style carbonaceous compressions? Is it not possible that other species will be discovered to be preserved in both Burgess Shale-style preservation as well as one of Conception, gravity cast, death mask, endorelief, or Khatyspyt preservation? In fact, as this paper was in preparation, Van Iten et al. (2013) proposed that certain Burgess Shale-style fossils of the Lantian biota from South China, originally described by Yuan et al. (2011), may actually be conulariids (or conulariid-like cnidarians) – which have also been reported from the 'Ediacara Biota' preserved as moulds and casts in sandstones (Ivantsov and Fedonkin, 2002; Van Iten et al., 2005).

Indeed, given that it is clear that certain so-called 'Ediacara Biota' specimens can also be preserved as Burgess Shale-style fossils, why should we wish to exclude them from the definition? Given the heterogeneous mixture of biological forms included in the 'Ediacara Biota' (more on which below), it is unclear why we should wish to exclude organisms fossilised in Burgess Shale-style taphonomy from consideration. It is worth noting that Conway Morris (1993) considered potential *Ediacaran*-like fossils from the Burgess Shale, while Xiao and Laflamme (2009, p. 32) specifically remarked on "the scarcity of *Ediacara* fossils in exceptionally preserved *Cambrian* biotas such as the *Burgess Shale*". So, *Cambrian* Burgess Shale-style fossils may be 'Ediacarans', but not *Ediacaran* Burgess Shale-style fossils? Clearly, there is an inconsistency here.

But, extending the use of the term 'Ediacara Biota' to include Burgess Shale-style fossils in the definition, without introducing an additional condition (either stratigraphic or biologic), would include the fossils of the Burgess Shale, Chengjiang, and Sirius Passet Lagerstätten, and many other sites, in the 'Ediacara Biota' –

which would render the phrase somewhat meaningless. Would we really ever consider *Laggania* or *Marella*, for example, as an 'Ediacaran'? A stratigraphic restriction could, of course, leave these *Cambrian* sites out of consideration, but then what of 'Ediacara-type' fossils in *Cambrian* sediments (Jensen et al., 1998; Crimes and McIlroy, 1999; Hagadorn et al., 2000) – or those predating the *Ediacaran* (Nagovitsin et al., 2008; Meert et al., 2011)? Further, if Precambrian Burgess Shale-style fossils were included in the 'Ediacara Biota', then why not fossils in other taphonomic styles? Essentially, such a definition would no longer be based on taphonomy, but purely on age, which – as discussed above – is not how the term has been used.

The fact that various authors (e.g. Conway Morris, 1993; Xiao and Laflamme, 2009) have considered the possibility of 'Ediacara-type' fossils in *Cambrian* Burgess Shale-style Lagerstätten makes clear, in fact, that the extra condition implied in the term is actually biological in nature. What would distinguish an 'Ediacaran' in the Burgess Shale from problematic Burgess Shale taxa like *Siphonotum*, *Herpetogaster*, or *Eldonia*? Should we only consider Burgess Shale-style fossils as 'Ediacarans' once conspecific specimens are found preserved as moulds and casts in siliciclastic, volcanoclastic, or carbonate sediments? What about congeneric, or confamilial specimens? How closely related would Burgess Shale-style specimens have to be to specimens preserved in one of the other taphonomic modes before we consider them to be 'Ediacara-type' fossils? The enigmatic *Eldonia* is a case in point, as not only is it known from the Burgess Shale (Walcott, 1911; Durham, 1974), but a specimen of *Eldonia* has also been described preserved as a siliciclastic mould and cast from the *Cambrian* of Siberia (Friend et al., 2002), and other eldoniids are also known as sandstone casts. Yet *Eldonia* has never been considered an 'Ediacaran'. So, a distinction has clearly been drawn whereby the possibility exists that 'Ediacarans' could be present in the Burgess Shale, but none of the presently known Burgess Shale taxa are widely considered as 'Ediacarans' – yet this distinction is drawn neither on age nor on taphonomy.

Is this not entirely abandoning a taphonomic definition for the term 'Ediacara Biota', and accepting a purely biological definition?

3.4. The biology-based definition

As discussed above, historical interpretations (Sprigg, 1947; Glaessner, 1984; Gehling, 1991) regarded the 'Ediacara Fauna' as the ancestors of familiar metazoan phyla. Seilacher (1984, 1989, 1992) challenged this interpretation, postulating the existence of an extinct Precambrian non-metazoan Kingdom. Zhuravlev (1993) regarded the 'biota' as xenophyophore protists (an interpretation with which Seilacher later agreed: see Seilacher et al., 2003), and Retallack (1994) proposed that they were lichens – a bizarre interpretation which was rapidly convincingly dismissed (Waggoner, 1995).

While these non-metazoan interpretations differ considerably, they share a significant common theme, in that they treated the entire 'Ediacara Biota' as a single, biologically coherent group or clade. If this was indeed the case, then the use of the term could be supported on that basis. However, we now know that this is incorrect. It is clear that what has been considered to be the 'Ediacara Biota' is a heterogeneous mixture of many different groups of organisms, including possible poriferans, cnidarians, and bilaterians as well as unequivocally extinct lineages (Gehling, 1987, 1988; Gehling and Rigby, 1996; Fedonkin and Waggoner, 1997; Narbonne, 2004; Fedonkin et al., 2007a; Gehling and Narbonne, 2007; MacGabhann, 2007; Flude and Narbonne, 2008; Laflamme et al., 2009; Xiao and Laflamme, 2009; Erwin et al., 2011; Vickers-Rich et al., 2013). There is no unified biological interpretation, nor

are these fossils which have been included in the ‘Ediacara Biota’ biologically distinct from other contemporaneous forms, as discussed in the preceding sections.

It is not even possible to regard the ‘Ediacara Biota’ as distinct due to their soft-bodied nature. Aside from the fact that such a definition would include soft-bodied fossils preserved in Burgess Shale-style or other taphonomic modes, which have not traditionally been included, it is now known that at least some fossils at Ediacara were in some way skeletal (Clites et al., 2012). Yet other skeletal fossils of Ediacaran age (e.g. *Cloudina*, *Namacalathus*, *Sinotubulites*) are not included in the ‘Ediacara Biota’ (Germs, 1972; Grotzinger et al., 2000; Amthor et al., 2003; Chen et al., 2008; Wood, 2011).

A biological definition for the term ‘Ediacara Biota’ therefore cannot be sustained.

4. What’s in a name?

As neither geographic, stratigraphic, taphonomic, or biological definitions of the ‘Ediacara Biota’ are internally consistent nor used consistently, it is clear that the term has lost all useful meaning. While this may appear to be simply quibbling over the use of a name, there are in fact significant implications. Previous use of the term ‘Ediacara Biota’ (or variants thereof) has actually led to several major errors and misconceptions, for two reasons.

First, because applying the term ‘Ediacara Biota’ to a particular (and internally inconsistent) group of fossils serves to separate these fossils from other contemporaneous specimens, implying that they are somehow different or special. As discussed above, in this case, they are not. It is worth considering the possibility that the historical use of the term ‘Ediacara Biota’ is one of the principal reasons for the hypotheses, discussed above, which placed a single biological interpretation on all included specimens. While such suggestions fuelled an ‘interesting’ two decades of notoriety, and even celebrity, for certain fossils of Ediacaran age, this undoubtedly held back the progress of Ediacaran palaeontology, as efforts were necessarily expended on dismissing unfounded and wildly speculative hypotheses (see, for example, Waggoner, 1995).

Second, by virtue of the concentration on the fossils considered as part of the ‘Ediacara Biota’, other Precambrian specimens have received far less than their due share of attention. This has had a severe impact on theories relating to the early evolution of the Metazoa, the biological interpretation of Ediacaran-aged organisms, and consideration of the biological change across the Precambrian–Cambrian boundary.

4.1. A terminal Precambrian mass extinction?

Seilacher (1984) not only proposed that the ‘Ediacara Biota’ represented an extinct Kingdom (Vendobionta), but also that this Kingdom became extinct in a mass extinction at the end of the Precambrian. Since then, various other authors have discussed the possibility of a terminal Precambrian mass extinction. For example, Crimes et al. (1995) described discoidal structures from the Booley Bay Formation in southeastern Ireland as “typical representatives of the Ediacaran fauna” (p. 106), claiming that these fossils provided “further links across the Precambrian–Cambrian boundary” (p. 106), and thus arguing against a terminal Precambrian mass extinction. Jensen et al. (1998) described “Ediacara-type fossils in Cambrian sediments” (p. 567) of the Uratanna Formation, South Australia, and likewise used these as evidence against an extinction event, stating “This discovery of Swartpuntia-like fronds, within beds burrowed by *T. pedum*, is compelling evidence that Ediacara-type organisms (and preservation of them) extended into the Cambrian period... the existence of the Uratanna fronds shows that there was not a complete

destruction of these Ediacara-type forms at the end of the Proterozoic” (p. 569). Crimes and McIlroy (1999) later described “an Ediacaran fauna” (p. 633) from the Cambrian of the Digermul Peninsula in Norway, claiming “These discoveries add to a growing body of evidence that some elements of the dominantly Neoproterozoic Ediacara fauna continue into the Phanerozoic, thereby diminishing the scope of a possible late Neoproterozoic mass-extinction event”.

MacGabhann et al. (2007) re-examined the Irish Cambrian fossils and found no evidence to suggest a biological connection between the Irish material and any specimens of Ediacaran age, claiming that their reinterpretation “would add considerable weight to proposals that the Ediacaran biota became extinct in a mass extinction at the end of the Ediacaran Period”.

Most recently, Laflamme et al. (2013) outlined the evidence for biological change across the Precambrian–Cambrian boundary, considering three hypotheses: a mass extinction at the Precambrian–Cambrian boundary; a biotic replacement scenario, whereby Cambrian forms gradually replaced the ‘Ediacara Biota’; and an aptly-named Cheshire Cat model regarding the apparent extinction as a taphonomic artefact (following Gehling, 1999). To consider these competing scenarios, Laflamme et al. (2013) reviewed the biogeographic distribution, stratigraphic distribution, and ecology of the Ediacara Biota, and tentatively concluded that based on presently available evidence, biotic replacement by ecosystem engineering appears to be the most likely cause for an ostensibly gradual extinction.

All of these analyses are fundamentally flawed. Leaving aside the fact that several of these papers discussed only discoidal fossils (Crimes et al., 1995; Crimes and McIlroy, 1999; MacGabhann et al., 2007) which even regardless of anything herein are difficult to regard as typical ‘Ediacara-type fossils’ due to their simplicity and undoubted paraphyly (although I unfortunately fell partially into that particular trap in MacGabhann, 2007), or that some of the ‘fossils’ described by Crimes et al. (1995) and Jensen et al. (1998) turned out to be sedimentary structures (Jensen et al., 2002; MacGabhann et al., 2007), none of these papers considered any fossils preserved in any style other than moulds and casts – no phosphatised specimens, no Burgess Shale-style specimens, no other taphonomic mode at all.

I will restate that in plainer language just to drive the point home – these authors all discussed the possibility of a terminal Precambrian mass extinction without considering the fate of all of the macroscopic fossils known from the Ediacaran.

It is clear that the use of the term ‘Ediacara Biota’ has served to artificially separate life in the Ediacaran and Cambrian, and led directly to flawed considerations such as those discussed above. In fact, this is abundantly clear from the very title of Laflamme et al. (2013)’s article: “The end of the Ediacara biota: Extinction, biotic replacement, or Cheshire Cat?”. Would we discuss the extinction of the Burgess Shale Biota, or the Solnhofen Biota, or the Hunsrück Biota? No, of course, not, because these are taphonomic terms, and are not in any way connected to the particular generic or specific composition of such fossil assemblages. We can even discuss the presence of Burgess Shale-style preservation in the Precambrian, although such fossil assemblages do not contain *Marella*, or *Eldonia*, or *Hallucigenia*, or *Laggania*, or any other taxon present in the Burgess Shale itself.

Laflamme et al. (2013)’s discussion of the Cheshire Cat model, the postulated taphonomically-controlled disappearance of a purportedly taphonomically-defined biota, is a particular case in point, especially as they dismiss this model. If the ‘biota’ is taphonomically-defined, as they state, then of course its disappearance must be taphonomically-controlled, by the very definition. The hypotheses of ‘biotic replacement’ or ‘mass extinction’ are completely contradictory to the taphonomic definition. In fact, implicit in

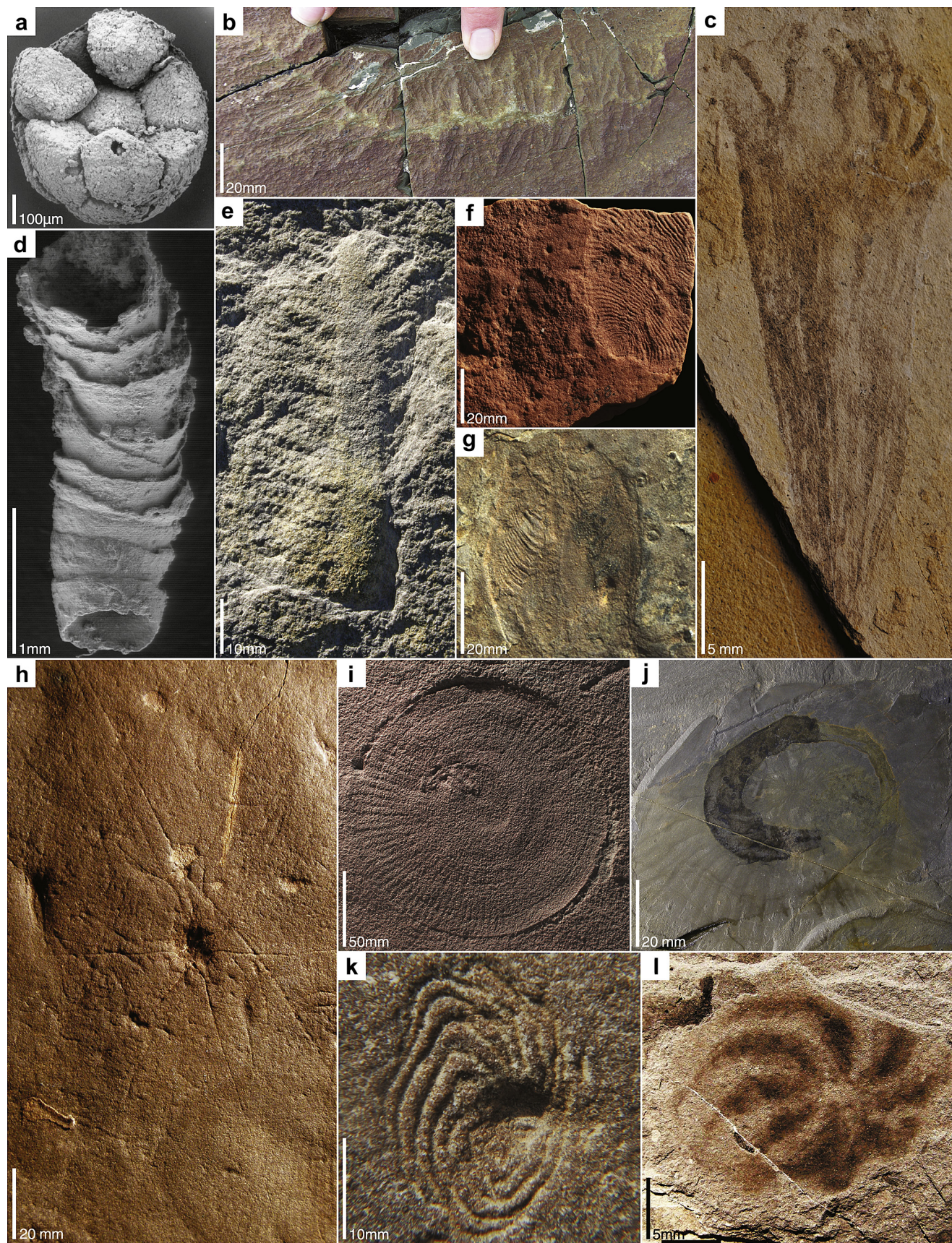


Figure 1. Spot the 'Ediacarans'. (a) *Parapandorina raphospissa*, a phosphatised metazoan embryo from the Doushantuo Formation, Weng'an, Guizhou, South China. SRA-1, 294. Photograph courtesy of Shuhai Xiao. (b) *Fractofusus*, a rangeomorph, preserved under volcanic ash from the Ediacaran of Newfoundland. Field photograph, courtesy of L.I. Flude. (c) Un-named putative conulariid (or conulariid-like cnidarian) preserved as a Burgess Shale-style compression from the Lantian biota, South China. NIGPAS-LT-295. Photograph

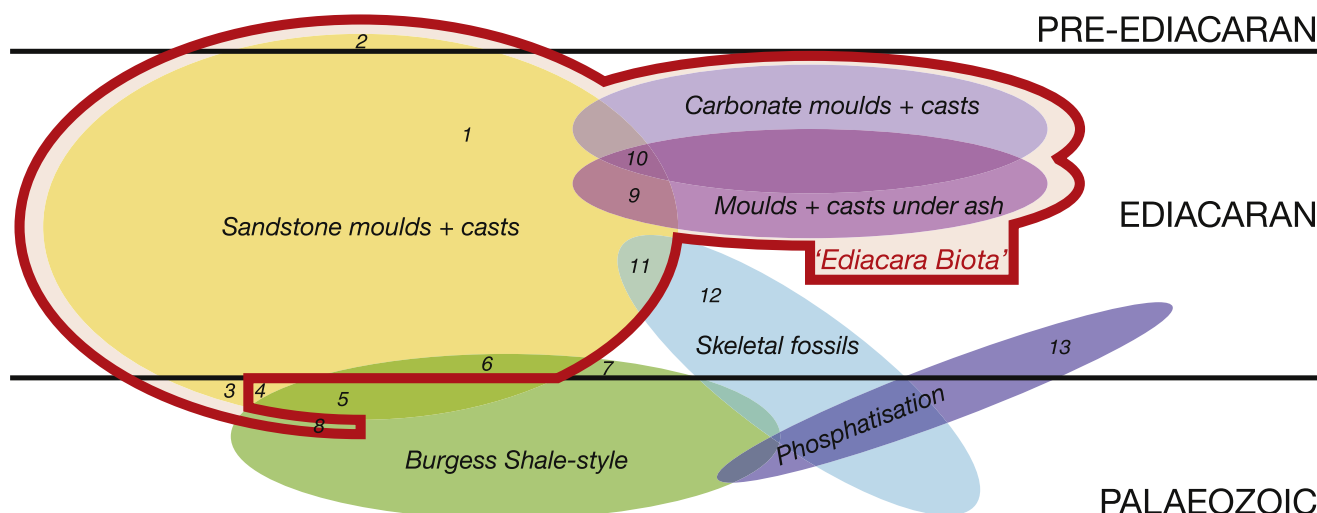


Figure 2. Venn-style diagram of the variety of styles of fossil preservation in the Precambrian and Palaeozoic, showing the current use of the term 'Eidacara Biota' (everything inside the red line). Numbers refer to particular fossils or groups of fossils – 1, Non-mineralised Eidacaran sandstone cast fossils, such as *Dickinsonia* (Fig. 1f). 2, Pre-Eidacaran fossils preserved as sandstone casts, for example the discoidal fossils reported as “Eidacara fossils” by Meert et al. (2011). 3, Palaeozoic fossils preserved as sandstone casts and considered part of the 'Eidacara Biota', such as the putative fronds from the Uratanna Formation, South Australia (Fig. 1g), described as “Eidacara-type fossils in Cambrian sediments” by Jensen et al. (1998). 4, Other Palaeozoic fossils preserved as sandstone casts – such as *Protonympha* (Conway Morris and Grazhdankin, 2005), *Parasolia* (Lenz, 1980), *Patanacta* (Cherns, 1994), or *Plectodiscus* (Ruedemann, 1916) – are not considered part of the 'Eidacara Biota'. 5, Palaeozoic fossils known preserved both as sandstone casts and in Burgess Shale-style, such as the eldonids (Fig. 1i, j). These are not considered part of the 'Eidacara Biota'. 6, Fossils from the Eidacaran known preserved both as sandstone casts and in Burgess Shale-style, such as *Eoandromeda*; these are considered part of the 'Eidacara Biota'. 7, Fossils from the Eidacaran known only as Burgess Shale-style compressions, such as the Lantian forms described by Yuan et al. (2011) (e.g. Fig. 1c). These are not considered part of the 'Eidacara Biota'. 8, Fossils from the Palaeozoic known only in Burgess Shale-style preservation, for example *Thaumaptilon*, have been considered part of the 'Eidacara Biota'. 9, Fossils such as *Bradgatia* (Flude and Narbonne, 2008) and *Rangaea* (Fig. 1e) are known preserved both beneath volcanic ash, and as sandstone casts. 10, *Charnia* is known preserved beneath volcanic ash, as a sandstone cast, and preserved in carbonates. 11, Skeletal fossils of Eidacaran age known from sandstone casts, such as *Coronacollina* (Fig. 1h), are considered part of the 'Eidacara Biota'. 12, Skeletal fossils of Eidacaran age such as *Cloudina* (Fig. 1d) are not considered part of the 'Eidacara Biota'. 13, Phosphatised fossils of Eidacaran age, including metazoan embryos (Fig. 1a), are not considered part of the 'Eidacara Biota'.

Laflamme et al. (2013)'s definition and discussion is the unwritten (and likely unintentional) understanding that the 'Eidacara Biota' is biologically different from contemporaneous and subsequent fossil assemblages preserved in different taphonomic modes.

If we consider the biotic change across the Precambrian–Cambrian boundary including those fossils excluded from these previous analyses, would the conclusions change? Perhaps. Certainly, as Burgess Shale-style preservation is known from both the Eidacaran and the Cambrian, the biotic change evident in fossils preserved in this style of preservation cannot be readily explained by invoking a Cheshire Cat-style taphonomic artefact. Such a hypothesis for the Eidacaran–Cambrian transition may therefore be unlikely. Is the evidence, when all taphonomic modes are included, sufficient to evaluate the possibility of a terminal Precambrian mass extinction? More data is likely required, but certainly a revised analysis including these previously excluded specimens is now needed to further our understanding of the biotic change in the late Eidacaran and early Cambrian.

4.2. The early evolution of the Metazoa, and life in the Eidacaran

Similarly, the focus on the arbitrary group of fossils considered to be part of the 'Eidacara Biota' to the exclusion of contemporaneous taphonomically dissimilar assemblages has strongly held

back evaluations of life in the Eidacaran in general, and most particularly consideration of the early evolution of the Metazoa.

Narbonne (2005) provided an excellent and authoritative review of the 'Eidacara Biota', entitled “*The Eidacara Biota: Neoproterozoic origin of animals and their ecosystems*”. Unfortunately, however, neither Khatyspyt-style preservation in carbonates nor Burgess Shale-style preservation in shales was considered at all (though in fairness, it should be pointed out that Khatyspyt-style fossils had, at that point, been described only in the Russian language literature), while discussion of skeletal and phosphatised fossils was each limited to a single short paragraph (pp. 423 and 436, respectively).

Xiao and Laflamme (2009) likewise reviewed Eidacaran palaeontology, in a paper entitled “*On the eve of animal radiation: phylogeny, ecology and evolution of the Eidacara biota*”. Nowhere in this article were compressions in shales or phosphatised specimens discussed, although they did note “*To fully resolve their phylogenetic affinities, future investigations should focus on exploring diverse taphonomic windows, including carbonaceous shales, carbonates and cherts, which might provide complementary morphological, taphonomic and ecological insights*” (p. 38).

Fedonkin et al. (2007b) published a wonderful book on Eidacaran palaeontology containing a wealth of useful information, entitled “*The Rise of Animals: Evolution and Diversification of the Kingdom Animalia*”. This book contains individual chapters on the

courtesy of Shuhai Xiao. (d) *Cloudina* from the Lijiagou section, uppermost part of the Dengying Formation, Shaanxi Province, South China. Courtesy of Yaoping Cai. (e) *Rangaea* preserved in endorelief within a sandstone event bed from Farm Aar, Kliphoeck Member of the Dabis Formation, Namibia. Reproduced from Vickers-Rich et al. (2013), Fig. 7.1, used with permission from the Paleontological Society. (f) *Dickinsonia* preserved as a negative hyporelief sandstone mould from the Eidacaran Eidacara Member, Brachina Gorge, South Australia. YPM 35458. (g) Frondlike specimen from the Cambrian Uratanna Formation, South Australia. Photograph courtesy of James Gehling. (h) *Coronacollina* from Bathtub Gorge, Eidacaran, South Australia. Holotype, SAM P43257, photograph courtesy of Erica Clites and James Gehling. (i) *Discophyllum*, an eldonid, preserved as a negative epirelief sandstone mould from the Ordovician First Bari Group, Tafilalet Lagerstätte, southeastern Morocco. (j) *Eldonia* preserved as a shale compression from the Cambrian Burgess Shale of Canada. USNM 193886. (k) *Eoandromeda*, preserved as a gravity cast from Eidacara, South Australia. NP01. Photograph courtesy of Shuhai Xiao. (l) *Eoandromeda*, preserved as a Burgess Shale-style compression, from the Doushantuo Formation, Wenghui, South China. ELRC-D-001. Photograph courtesy of Shuhai Xiao.

Archean and Proterozoic, and on the 'Ediacara Biota' from the Mistaken Point biota of Newfoundland, from the Nama biota of southern Africa, from the Ediacara Hills of South Australia, from the White Sea Lagerstätte in northern Russia, from Podolia in Ukraine, from the Olenek Uplift in Siberia, from the Central Urals, and from northwestern Canada. Other sites are considered in a single chapter, including localities in England, Wales, the United States, South America, and China. Discussion of Burgess Shale-style fossils in the Ediacaran occupies less than two pages of the subsection on China (p. 196–197). Discussion of phosphatised fossils likewise occupies less than two pages of the same subsection (p. 197–198).

Most recently, molecular clock dates for the early evolution of various metazoan clades were presented by [Erwin et al. \(2011\)](#), and compared to the early fossil record. They presented a revised classification of Precambrian fossils, proposing that six definite clades (Rangeomorpha, Erniettomorpha, Dickinsoniomorpha, Arboreomorpha, Triradialomorpha, and Kimberellomorpha) and three likely clades (Bilateralomorpha, Tetraradialomorpha, and Pentaradialomorpha) could be identified in the Ediacaran, in addition to the paraphyletic Porifera. However, nowhere in their work were any Ediacaran Burgess Shale-style fossils considered; skeletal Ediacaran fossils were only briefly mentioned.

All of these works are extremely useful, and have undoubtedly advanced the field. Despite that, however, by limiting or omitting discussion of fossils preserved in a diverse range of taphonomic modes, all of them are in one respect fundamentally flawed. How can we discuss the early evolution of the Metazoa without considering all of the oldest known potentially metazoan fossils? The Lantian fossils preserved in Burgess Shale-style described by [Yuan et al. \(2011\)](#) and other taphonomically similar assemblages predate most of the widespread assemblages of the so-called 'Ediacara Biota', and are strongly deserving of treatment in such works, especially given suggestions that some of these fossils may represent metazoans in the form of conulariids ([Van Iten et al., 2013](#)). Similarly, phosphatised microfossils include specimens proposed to be metazoan embryos ([Dornbos et al., 2005](#); [Donoghue et al., 2006](#); [Hagadorn et al., 2006](#); [Yin et al., 2007, 2013](#)). Evidence for early metazoan life may also come from other sources, such as fossil biomarkers, which have been suggested to record the Cryogenian evolution of poriferans ([Love et al., 2009](#)).

Any discussion of the early evolution of the Metazoa without considering all metazoan fossils or evidence is, of course, unfinished. Yet no review or discussion has ever included all the evidence, due principally to a concentration on fossils considered to be part of the 'Ediacara Biota'. Our picture of the early evolution of the Metazoa therefore remains incomplete.

5. Conclusions

The term 'Ediacara Biota' (or variants thereof) no longer has any meaning. It is not taphonomically consistent, not biologically consistent, not stratigraphically or geographically consistent; indeed, it is not internally consistent by any potential definition. As currently understood ([Figs. 1 and 2](#)), it excludes other soft-bodied forms while including at least one skeletal form (and excluding other skeletal forms). It includes all fossils preserved in death mask, gravity cast, endorelief, Conception, or Khatyspyt styles, but excludes specimens of the same species preserved in different taphonomic modes. It includes specimens from Cryogenian and Cambrian sediments, but excludes many Ediacaran-aged fossils. It artificially singles out an arbitrary, now-incoherent group of fossils, and incorrectly implies that they are somehow biologically distinct from contemporaneous or succeeding assemblages. It is a term that has lost its meaning.

The historical use of the term has entrenched the notion of the individuality of the 'Ediacara Biota', and while once the term had a clearly understood basis, time and new discoveries have rendered the term essentially meaningless, with the realisation that Ediacaran Lagerstätten preserve a heterogeneous mixture of many different kinds of organism in a variety of taphonomic styles. So, why distinguish one (now-arbitrary) group of fossils from all other contemporaneous remains?

In the future, it is recommended that the term 'Ediacaran' should be used in a purely stratigraphic sense, such that 'Ediacaran fossils' refers solely to fossils from strata of the Ediacaran System, regardless of mode of preservation, biological affinity, geographical location, or any other factors. Terms such as 'vendobiont', 'rangeomorph', and other names such as those introduced by [Erwin et al. \(2011\)](#) may be used to refer, biologically, to definite or likely clades – regardless of stratigraphic position, taphonomic style, or geography. Locality-based terminology such as 'Nama biota' or 'Mistaken Point biota' can be used geographically, to refer to fossil assemblages from particular localities, regardless of taphonomy, stratigraphic position, or biological affinity (for the sake of avoiding confusion, it may be best if the term 'Flinders biota' is used to refer to the South Australian fossils, to avoid the potential for confusion with previous usage of 'Ediacara Biota'). Taphonomic terms used herein introduced by [Gehling \(1999\)](#), [Narbonne \(2005\)](#), [MacGabhann \(2007\)](#) and others – such as 'death mask', 'gravity cast', 'Flinders-style', 'Conception-style', positive or negative epirelief or hyporelief, etc. – are sufficient to refer to fossils preserved in a particular taphonomic style or styles, without reference to stratigraphic position, biology, or geography. General reference to fossils preserved as moulds and casts in siliciclastic, volcanoclastic, or carbonate sediments may be made by the use of a term such as 'sediment replica'.

It is time to retire the term 'Ediacara Biota', to stop talking about 'Ediacarans', and to start talking about the real diversity, disparity, taphonomy, biology, biostratigraphy, evolution, and extinction of *all* the fossils of the Ediacaran System.

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